Horizontal and vertical movements as predictors of foraging success in a marine predator

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Horizontal Area-Restricted-Search and Vertical Diving Movements to Predict Foraging Success in a Marine Predator

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Abstract

With technical advances in wildlife telemetry, the study of cryptic predators' responses to prey distribution has been revolutionised. Considering marine predators, high resolution tagging devices were developed lately to collect long and precise diving datasets. In this study, we investigated, at fine temporal and spatial scales, changes in the horizontal movements and diving patterns of a marine predator, the southern elephant seal. Satellite tracking data collected on nine seals were processed with switching state-space models. Seals' body condition, as a proxy for foraging success, was estimated through changes in drift rate from Time Depth Recorder (TDR) data. We identified (1) statistically distinct behavioural modes along the

tracking data (intensive vs. extensive foraging modes) and (2) dive classes from the TDR diving data (drift, exploratory, shallow active and deep active dives). Mass gain over the animals' foraging trip was also linked with the proportions of intensive foraging zones and dive classes. Active dives, associated with vertical foraging and chasing, were more numerous when the seals were in intensive foraging mode. Improved body condition and mass gain of seals were also associated with the occurrence of intensive foraging mode and, within the vertical dimension, with sets of highly active dives. In conclusion, proportions of dive classes displayed by the seals proved to vary according to their horizontal behaviour. The results allow us to conclude that intensive foraging detected from surface tracking data is a good predictor of the diving activity and foraging success occurring in the vertical dimension.

Keywords: area-restricted search, dive classification, drift dive, fine scale behaviour, movement analysis

1 Introduction

Understanding the responses of predators to spatial and temporal variability of their prey distribution is fundamental for determining how animals may respond to global changes in their environment. The Southern Ocean is one of the most productive oceans (Smetacek & Nicol, 2005) and it has been shown that this circumpolar ocean has warmed more rapidly than the global ocean average (Gille, 2002). It has also been shown that winds over this ocean have strongly increased over the past few decades (Meredith & Hogg, 2006) causing an increase in eddy activity and number. This could have significant impacts on primary productivity (Le Quéré *et al.*, 2007) and hence on feeding opportunities for predators. Nonetheless, direct observations of how marine predators interact with their environment and their prey are very scarce. Because of the Southern Ocean remoteness, it is particularly challenging to obtain information on diet and the distribution of prey for long-ranging migrating species in those waters.

Acurate feeding indices are often difficult to obtain, and most studies instead use proxies such as changes in movement patterns and time spent within restricted areas (Weimerskirch *et al.*, 2007; Aarts *et al.*, 2008). Therefore, recent developments in animal-mounted loggers (Weimerskirch & Jouventin, 1990; Weimerskirch *et al.*, 2002) and indirect diet analyses (Bradshaw *et al.*, 2004) have significantly increased the amount of knowledge on cryptic marine predators' ecology. Especially, the recordings of predators' movements, diving behaviour and *in situ* oceanographic parameters have indirectly contributed in a better understanding of potential prey distribution otherwise difficult to observe.

By correlating movement patterns to environmental conditions, characteristics of the areas profitable for a predator can be revealed (Turchin, 1991). In various predator species, resource

acquisition has been linked to a type of free-ranging behaviour called the area-restricted search (ARS) (Kareiva & Odell, 1987). In a prey-aggregated environment, such as in the open ocean, an animal having already captured a first prey intensifies its foraging in the patch (Charnov, 1976; Parker & Stuart, 1976). Therefore, an ARS is characterised by a decrease in displacement speed and an increase in the track sinuosity in areas with putative prey aggregation (Bovet & Benhamou, 1988). Between two patches, the animal, on the contrary, travels more linearly and at a faster pace. Natural environments are generally considered as hierarchical patch systems, in which patches at small scales are nested in patches at larger scales (Kotliar & Wiens, 1990). While foraging, predators often display movement patterns at multiple spatial and temporal scales that are assumed to match the spatial structure of the hierarchical aggregations of prey (Fauchald, 1999). Since predators likely adjust their foraging movements at small spatial scales, especially within a dense patch, prey encounter rate is supposed to play a major role in predator's foraging decisions. On the other hand, past experiences are expected to act mainly in large-scale movements at a scale where prey distribution is more predictable (Hunt *et al.*, 1999). With the latest technical advances in wildlife telemetry, it is now possible to examine small-scale movements that are crucial to better understand scale-dependent adjustments of long-ranging predators. By using high-precision locating system (GPS, Weimerskirch *et al.* (2002)) together with high-resolution behavioural recorders (Time Depth Recorders (TDR) Charrassin *et al.* (2001), stomach temperature sensors Austin *et al.* (2006)), it is now possible to accurately study foraging decisions. However, to understand the effects of environmental variability on foraging success of marine predators and, ultimately their fitness increase, requires not only at-sea movement analyses, but also some method of identifying where and when the animals actually improve their body condition.

Considering diving predators, buoyancy has been proved to directly depend on the animals' body condition(Webb *et al.*, 1998; Aoki *et al.*, 2011). As a predator feeds and increases its body

condition, the relative proportion of adipose tissue increases thereby increasing its buoyancy (Robinson *et al.*, 2010). Therefore, a predator species that performs dives during which the animals drift passively in the water column can be considered as an ideal study model to inform on *in situ* buoyancy *in situ* (Biuw *et al.*, 2003). Travelling thousands of kilometres per year in the circumpolar waters of the Southern Ocean (McConnell *et al.*, 1992), southern elephant seals, *Mirounga leonina*, are elusive marine predators that can spend as much as 85% of their lifetime at sea (McIntyre *et al.*, 2010). They continuously dive during their extended stay at sea and display behaviours qualified of "drift dives" along their track (Crocker *et al.*, 1997). They regularly perform those dives during which they stop swimming and drift passively in the water column (Biuw *et al.*, 2003; Mitani *et al.*, 2010). Vertical movements during these dives were shown to be related to the seal's body condition (Webb *et al.*, 1998): fat and positively buoyant seals will follow an upward drift. Inversely, lean seals with negatively buoyant body condition will sink during a drift dive. An increase in the drift rate over time is therefore an index of a successful foraging activity (Biuw *et al.*, 2007; Bailleul *et al.*, 2007b; Thums *et al.*, 2008; Robinson *et al.*, 2010). Although there are potential errors in the estimation of foraging success from drift rate, they generally lead to an underestimation of the energy gain and foraging success (Robinson *et al.*, 2010). Southern elephant seals represent therefore a unique opportunity for studying, *in situ*, links between the foraging behaviour and the individual's body condition.

Horizontal foraging behaviour, from track-based analyses of low-resolution surface tracking data, has been studied in detail (Bailleul *et al.*, 2008). However, southern elephant seals spend little time at the surface between each dive (Hindell *et al.*, 1991) and feed on deep-ranging prey (Cherel *et al.*, 2008). In addition, previous studies could only integrate the diving behaviour by using indices estimated from low-resolution dive profiles (four depth-time points per dive, Biuw *et al.* (2003); Bailleul *et al.* (2007a)). Recent studies have focused on the fine scale vertical

behaviour which is more likely to respond directly to prey abundance (Thums *et al.*, 2011). However, fine scale vertical as well as horizontal foraging behaviour remain poorly known which limits our understanding of the seals' responses to the variability in prey distribution.

In the Southern Ocean, mesoscale features, such as fronts and eddies, have been shown to have a significant impact in structuring and enhancing primary productivity (Bakun, 2006). They are likely to influence the spatial structure of prey patches and play a key role in the formation of profitable foraging areas for oceanic predators (Bost *et al.*, 2009). The interfrontal zone, between the Polar Front (PF) and the Subtropical Front (STF, see Figure 1), is especially dynamic with locally productive eddies that are rich in prey. Within the Kerguelen population, Bailleul *et al.* (2010a) work suggests that over two thirds of the southern elephant seal females forage in the interfrontal zone. It is therefore likely to be a key habitat where those predators interact with spatially and temporally heterogeneous oceanographic features (Dragon *et al.*, 2010). In this study, we used high resolution tracking and diving data to investigate fine-scale temporal and spatial changes in horizontal movements and diving patterns of female elephant seals in the interfrontal zone. We expected a good correspondence between the areas of intensive foraging identified from horizontal tracking data and the areas with high proportions of foraging dives, as determined from TDR data. Finally, using drift rate as a physiological proxy of foraging success, we expected to monitor the gain or loss in the seals' body conditions and to relate it with the observed diving behaviour.

2 Material & Methods

2.1 Logger Deployment

In October 2009, nine post-breeding southern elephant seal females, all about the same mass (296 ± 26 kg) and length (236 ± 14 cm), were captured on the Kerguelen Islands (49°20'S, 70°20'E). They were anaesthetised using a 1:1 combination of Tiletamine and Zolazepam (Zoletil 100) which was injected intravenously (McMahon *et al.*, 2000). Data loggers were glued on the head of the seals, using quick-setting epoxy (Araldite AW 2101), after cleaning the fur with acetone. Four seals were equipped with satellite-GPS loggers in combination with satellite-Argos and archival data loggers (MK10 Fast-Loc, Wildlife Computers, Washington, USA). MK10 devices transmitted Argos location data and collected GPS location data. To save battery life, the sampling interval of GPS locations was set to a minimum of 20 minutes, i.e. slightly shorter than the average dive duration of the species (Hindell *et al.*, 1991). The additional logger, Time-Depth Recorder (TDR), included in the MK10 devices collected and archived pressure and temperature levels every two seconds. Five other seals were equipped with Fluorometry - Conductivity - Temperature - Depth Satellite - Relayed Data Loggers (termed Fluo-CTD-SRDLs, designed and manufactured by the Sea Mammal Research Unit, University of St Andrews, Scotland) combined with MK9-TDR loggers (Wildlife Computers, Washington, USA). Fluo-CTD-SRDLs devices allowed the calculation and transmission of tag positions estimates of Argos quality. The MK9 devices combined with each Fluo-CTD-SRDL were set to sample and archive pressure and temperature levels every two seconds. After locating their respective haulout beaches via Argos locations, returning females were recaptured, weighed and loggers were retrieved.

2.2 Tracking data and identification of horizontal foraging behaviour

The GPS and Argos seal tracking data were both analysed with state-space models in order to detect areas of restricted search (Jonsen *et al.*, 2003; Patterson *et al.*, 2008; Schick *et al.*, 2008; Block *et al.*, 2011). Argos locations were first estimated using the observation model of a switching-state-space model in order to take into account measurement errors (Jonsen *et al.*, 2003). Following preliminary studies based on the movement parameters distributions (not displayed here), we used two behavioural modes for the analyses. The state-space models also estimated the probability of being in a particular behavioural mode (intensive foraging, that is when ARS behaviour is displayed, vs. extensive foraging, when the animal travels at a faster and more linear pace) along the animals' paths (for details see Jonsen *et al.* (2007); Block *et al.* (2011)). GPS tracks were analysed the same way: the switching state-space models discerned two behavioural modes within the location data. All models were fitted with freely available software *WinBUGS* (Bayesian Analysis Using Gibbs Sampler, Spiegelhalter *et al.* (1999)) called from *R* (`R Development Core Team`, 2009) with the package *R2WinBUGS* (Sturtz *et al.*, 2005). As recommended by Dennis (1996), we used vague priors (Gamma and Uniform distributions). Two Monte-Carlo Markov Chains (MCMC) were run for each model, with 50000 iterations following a 25000 burn-in (thin=2).

As female southern elephant seals from Kerguelen population are known to forage mostly in the pelagic waters of the interfrontal zone (Bailleul *et al.*, 2010b; Dragon *et al.*, 2010), we focused on the pelagic part of the tracks after having applied a bathymetric mask (1000 m depth from Etopo mask 2' (NGDC, 2001)) to exclude all locations on the Kerguelen and Crozet plateaux, and hence all benthic dives.

2.3 Diving Behaviour and dive classification

The following diving variables were derived from MK9 and MK10 TDR data (Table 1): maximum depth, descent and ascent speeds, bottom-time duration (where the bottom phase starts at the end of the descending phase and finishes at the beginning of the final ascent to the surface) and bottom-time residuals (residuals of multiple regression of $bottomtime \sim maximumdivedepth + diveduration$ Bailleul *et al.* (2008); calculated for each dive within a path) and vertical sinuosity in the bottom phase (Equation 1, derived from Weimerskirch *et al.* (2007)).

$$BottomSinuosity = \frac{BottomDistance_{observed}}{BottomDistance_{euclidean}} \quad (1)$$

where $BottomDistance_{observed}$ is the total vertical distance swum in the bottom of the dive, and $BottomDistance_{euclidean}$ is the sum of the Euclidean distances from the depth at the beginning of the bottom to the maximum depth and from the maximum depth to the depth at the end of the bottom phase.

Vertical sinuosity takes a value of 1.0 when the animals swims in a straight path at the bottom of its dive. Any deviation from a straight path increases the sinuosity value. The horizontal distance travelled during each dive was also estimated from linearly interpolated GPS tracking data. Drift dive identification was processed from the complete time-depth (TDR) data in 3 steps. (1) Instantaneous vertical speed was calculated from the time-depth data. (2) Vertical speed was then smoothed by using a moving average filter (10 seconds window) in order to compensate for abrupt changes in depth reading due to the sensor accuracy ($\pm 1m$). (3) Within dives, drift phases were isolated using a custom-made function under R software (`R Development Core Team`, 2009). Drift phases were detected as periods of time of more than 3 minutes during which the vertical speed was bounded between $[-0.6; 0.6] m.s^{-1}$ and with a low variance ($s^2 < 0.005$) (for more details see the annotated *R* codes in the supplementary

material). For each drift dive, a drift rate was determined as the slope coefficient of a linear regression between depth and time (Biuw *et al.*, 2003; Bailleul *et al.*, 2007a; Mitani *et al.*, 2010). Daily averaged drift rates were calculated for the 3-month tracks.

Following a preliminary analysis of diving behaviour (Table 1) and a literature review (Hindell *et al.*, 1991; Schreer *et al.*, 2001; Hassrick *et al.*, 2007), four dive classes displayed by the seals in pelagic waters were determined. A k-mean classification was then applied on the normalised Principal Component Analysis (PCA, in this study with 4 principal components) scores from the behavioural variables of all individuals in the pelagic part of their tracks (Forgy, 1965). Transition matrices including the probabilities of dive class changing were then estimated. The daily proportions of each dive classes for each individual were also calculated. Linear mixed models, with individual as random effect, were used to evaluate the daily proportions of dive class in intensive foraging vs. extensive foraging areas detected from the tracking data (in R, nlme library from Pinheiro & Bates (2000) with REML method). Models' assumptions were verified and no autocorrelation nor heterogeneity of variance of within-group residuals was noticed (Pinheiro & Bates, 2000).

2.4 Detection of successful foraging areas with drift rate increases and mass gain models

Positive variations of drift rate are supposed to indicate an improvement of the seal's body condition and buoyancy (Crocker *et al.*, 1997; Biuw *et al.*, 2003). We used increases in drift rate as a physiological index of successful foraging activity along the seals' tracks. The overall drift rate increase was calculated as the difference between the mean drift rate over the last 10% of the track, hereafter referred as the final drift rate, and the one over the first 10% of the track. Final drift rate before the animal's hauling out and percentage of time spent in intensive foraging were also considered. Finally, we also calculated the respective proportions of the four

dive classes while the animal was displaying intensive, or extensive, foraging behavioural mode. For all individuals, mass gain (kg) over the foraging trip was related, using linear models, to overall drift rate, final drift rate and the proportions of dive classes while in intensive foraging. In the end, we used linear models to estimate the mass gain from multiple regressions of the variables listed above. Model selection was based on Akaike Information Criterion (AIC, Akaike (1973), with a correction for small sample sizes Burnham & Anderson (2002)) to find the best linear model (Venables & Ripley, 2002).

3 Results

3.1 Statistics of the horizontal tracking data

Argos tags transmitted in average ($mean \pm s.d.$) 6.86 ± 4.31 locations per day whereas GPS tags collected an average of 38.28 ± 10.57 daily locations. The 9 animals equipped for this study spent an average of 79 ± 6 days at sea with 69 ± 9 days in the pelagic area. They covered an average of 4399 ± 622 km, including 3822 ± 763 km in pelagic waters (Figure 1). All but one individual foraged exclusively within the interfrontal zone east of Kerguelen Island. The last one went to the western interfrontal zone, near Crozet plateau. Individual seals dived on average 64 times per day which is consistent with the literature (Boyd & Arnbom, 1991). This provided 5059 ± 700 dives, per seal, of which 4529 ± 909 were in pelagic waters. From the state-space model analysis, seals displayed two statistically distinct behavioural movement modes: intensive, which corresponds to the display of ARS behaviour, and extensive foraging. Intensive foraging mode was estimated on average during 33 % of their time ($33 \pm 12\%; 28 \pm 8$ days) including in pelagic waters (23 ± 9 days).

3.2 Characterisation and localisation of the dive classes

For all individuals, four dive classes were detected and defined as: drift, exploratory, shallow-active and deep-active dives. The biological meanings of the dive classes will be discussed in detail in the first part of the discussion. Characteristics of the four dive classes are illustrated in Figure 2 and Table 2. Although their relative proportions varied, with for instance deep active dives being more numerous by day than by night, all dive classes were observed by day and night time (Figure 2b). Drift dives were the least sinuous in the bottom (Figure 2d), presented the longest bottom time durations (Figure 2a,c) and low horizontal distances (Figure 2f). While “drift-diving”, the animals displayed low descent (Figure 2e) and ascent speeds (Figure 2d) and performed this class of dive at average depths (Figure 2c and Table 2). On the

contrary, deep active and shallow active dive classes exhibited high sinuosity ratio during their bottom phases (Figure 2d). The deep active dive class was the most sinuous of all dive classes. Both shallow and deep active classes also exhibited high descent and ascent speeds (Figure 2d,e). Deep active dive presented also the lowest horizontal distance travelled between two dives of this class (Figure 2f). Finally deep active dive class was also characterised by negative bottom-time residuals that is bottom times lower than expected. Considering the exploratory dive class, they were characterised by large horizontal distance (Figure 2f), medium vertical sinuosity at the bottom of the dives (Figure 2d) and low descent speed (Figure 2e). Figure 3a presents the typical profiles of the four dive classes.

The proportions of dive classes along the pelagic part of the individual tracks are presented on Table 3. Deep active dives represent the majority of the dives along the animal path (46.1 % in average) while shallow active and exploratory dives are the second and third classes with respectively 31.3% and 14.9% of the dives. Finally, drift dives are sparsely displayed (7.7%). The combination of deep and shallow active classes (from now on referred as active dives) represents over three quarters of the whole set of dives (77.4 %). All dive classes occurred all along the tracks (Figure 3b). On the other hand, observed probabilities of dive class changing from dive at time t to dive at time (t+1) revealed a high temporal persistence, i.e. temporal auto-correlation, in the animals behaviour and a hierarchy in the dive classes activity (Table 4). An animal displaying a shallow active dive is more likely to continue displaying this class of dive or to change most likely for a deep active dive or an exploratory dive.

3.3 Combining horizontal foraging behaviour identified from tracking data to fine scale vertical behaviour

The most parsimonious linear mixed model on the daily proportions of shallow active dives showed a positive intercept ($intercept = 42.11 \pm 5.42$, p.value = < 0.0001), a negative link with

the daily horizontal distance travelled ($slope(Hor.Dist) = -0.26 \pm 0.03$, p.value = < 0.0001) and a positive link with the intensive foraging mode ($slope(ARS) = 5.32 \pm 2.35$, p.value = 0.02). Furthermore, the most parsimonious linear mixed model on the daily proportions of drift dives showed a positive intercept ($intercept = 5.91 \pm 1.28$, p.value = < 0.0001), a positive link with the proportions of shallow dives ($slope(Shallow.Active) = 0.03 \pm 0.01$, p.value = 0.03) and with the intensive foraging mode ($slope(ARS) = 1.37 \pm 0.73$, p.value = 0.05). Figure 4(a, b) confirm the variations of proportions of the four dive classes between the 2 behavioural movement modes detected on the tracking data: extensive (a) and intensive (b) foraging. The proportion of exploratory dives almost doubles in extensive foraging areas compared to intensive ones. Meanwhile, drift dives number is reduced nearly 50% in extensive foraging areas. The proportion of deep active dives remains identical while the proportion of shallow active dives increases with the intensification of the foraging behaviour. Therefore, the proportion of active dives, combination of deep and shallow active dives, is more important in intensive foraging areas than in extensive ones.

3.4 Mass Gain related to an increase in drift rate and active dives

Mass gain ranged from -60 to 120 kg (Figure 5) and was positively related to four variables. The overall change in drift rate along the track, referred as the gain in drift rate ($\rho = 0.83, p.value = 0.006$, Figure 5a), and the final drift rate ($\rho = 0.78, p.value = 0.013$, Figure 5a) were positively related to the mass gain. The proportion of time spent in intensive foraging ($\rho = 0.67, p.value = 0.049$, Figure 5b) and the proportion of active dives realised while the animal was in intensive foraging ($\rho = 0.80, p.value = 0.009$, Figure 5b) were also positively related to the mass gain. The drift rate gain was the variable best correlated with mass gain. The model selection, based on small sample size corrected AIC, that applied to the multiple regressions (table 5) highlighted the most parsimonious model: Mass Gain $\sim$ Drift Rate Gain ($AICc = 65.99$, $R^2 = 0.685$, with $slope = 708.26 \pm 181.54$ and

$intercept = -110.75 \pm 42.82$). It is to be noted that the second most parsimonious is: Mass Gain $\sim$ Drift Rate Gain + Proportion Active Dives in ARS ($AICc = 69.47$ and $R^2 = 0.728$).

4 Discussion & Perspectives

In this study, we showed that intensive foraging detected from surface tracking data is a good predictor of the diving activity and foraging success occurring in the vertical dimension. Previous studies have shown that southern elephant seals display several dive classes during the pelagic parts of their foraging trips (Hindell *et al.*, 1991; Schreer *et al.*, 2001; Thums *et al.*, 2008). However, only few studies linked the fine scale diving patterns with the horizontal movements detected from high resolution tracking data e.g. Thums *et al.* (2011). Our results suggest that proportions of active dives are more important when seals are displaying area-restricted search behaviour than when they are extensively foraging. Our study also highlights that the mass gain over the animals' foraging trip is positively correlated to the gain in drift rate and to the proportions of active dives and intensive foraging detected from tracking data.

4.1 Characterisation and ecological role of dive classes

In the pelagic waters of the interfrontal zone, all individuals displayed four distinct dive classes. For all individuals but one (09-78524, Table 3), the drift dives were the least abundant dives. As first mentioned by Hindell *et al.* (1991), drift dives occurred in bouts generally in the early hours of the morning and are thought to be resting and/or food processing dives (Crocker *et al.*, 1997; Mitani *et al.*, 2010). For some individuals, we also noticed a high occurrence of drift dives after long sets of deep active dives (results not shown). Thums *et al.* (2008) observed a tendency of positively buoyant seals to display upwards drift phases in their foraging dives leading to their misclassification as drift dives. Because our study was based on post-breeding

foraging trips that are much shorter (ca. 2 months) than post-moulting ones (ca. 8 months), only one seal reached positive buoyancy. Therefore, misclassification of the dives was not problematic in our study.

High sinuosity, corresponding to wiggle displays in the bottom phase, combined with a maximisation of the time spent at the bottom of the dive (i.e. high descent and ascent speeds) can be associated with intensively active foraging (Fedak *et al.*, 2001). Both deep and shallow active dives are very abundant, occur in bouts or series and generally have a uniform depth within a bout. Finally, deep active dives were characterised by negative bottom-time residuals corresponding to dives with short bottom duration in regards to their maximum depths. Large vertical sinuosity, fast descending and ascending speeds combined to negative bottom-time residuals highlight the very high energetic demand of this dive class. Shallow active dives presented slightly positive bottom-time residuals that is a longer time than expected at the bottom phase which was presented in previous studies as a proxy for intensive foraging (Bailleul *et al.*, 2007b). Considering the time spent at the bottom, female elephant seals seem to display a trade-off between foraging intensity and depths at which foraging occurs. Since bottom-time residuals are calculated with a linear multiple regression (Bailleul *et al.*, 2007b, 2008), it seems plausible that at deep depths, where the deep active dives occur, the relation between dive duration and maximum depth changes. The inflexion of this relation would therefore lead to the sign inversion observed in bottom-time residuals between the deep and shallow active dives. In shallow active dives, seals would optimise their efficient hunting time in maximizing the proportion of time spent at the bottom of their dives where prey may be encountered, hence displaying positive bottom-time residuals (Schreer et al. 2001). While deep-diving, the seals' abilities for bottom-time adjustment, on the contrary, are reduced by long descending and ascending durations. In the end, both active dive classes are likely to represent intensive foraging activity as square dives were described in previous studies on various diving predators (LeBoeuf *et al.*, 1988; Hindell *et al.*, 1991; Schreer & Testa, 1996;

Fedak *et al.*, 2001; Schreer *et al.*, 2001; Hassrick *et al.*, 2007). Therefore, the vertical sinuosity at the bottom was an important predictor of the dive class as speed and depth were in other classification studies on southern elephant seals (Hindell *et al.*, 1991; Thums *et al.*, 2008). Exploratory dives exhibited large horizontal distances and low bottom time residuals. These dives are thought to be travelling dives because the seals dive at average depths, without displaying much wiggle activity (low sinuosity in the bottom), with low-speed descent and ascent phases and potentially travelling in a straight direction (high horizontal distance). All these characteristics also describe the V-shape dives detected in previous studies (Schreer *et al.*, 2001).

Although southern elephant seal females from Kerguelen forage mainly in pelagic waters (Dragon *et al.*, 2010; Bailleul *et al.*, 2010b), it has been shown that females of this species can dive and forage over continental shelves (Hindell *et al.*, 1991). In this case, they can interact with different oceanographic conditions and display other foraging behaviours resulting in additional dive classes. As a result, our data correspond to a subset of the dive classes spectrum displayed by foraging seals. All seals in this study were females, so additional work on the fine-scale diving behaviour of males is needed.

4.2 Association of horizontal foraging patterns with vertical behaviour and overall successful foraging

Our results indicate that southern elephant seals display ARS over 30% of their time spent at sea and mainly within pelagic waters. From previous tracking studies, southern elephant seals are known to be predators that prospect continually within and between prey patches (Bailleul *et al.*, 2008; McIntyre *et al.*, 2011). This may be especially true for pregnant phocid females that exhibit a capital-breeding strategy. Phocids accumulate energy stores prior to fasting during month-long hauling-out for parturition or moult (Berta *et al.*, 2006). Between fasting periods

during parturition and moult, pregnant southern elephant seal females, on their 3-month post-breeding foraging trip, potentially optimise their foraging to recover from breeding and prepare the next energetically demanding period of hauling-out. All seals in this study showed a large proportion of active dives that occur all along the pelagic parts of the tracks by day and night time. This confirms that seals are foraging and probably feeding all along their tracks and that the typical intensification of their search in a zone may therefore correspond to encounters with high quality prey patches. Seals were also found to modify their proportions of dive classes according to the movement behavioural mode: while intensively foraging, the active dive classes were more represented, e.g. most energetically demanding dives (high vertical sinuosity and high ascent speed). The adjustment between intensive and extensive foraging behaviour was not observed on the proportion of deep active dives but on the shallow active ones. From a physiological point of view, numerous deep dives that require intense foraging activity could be too demanding in terms of recovery time (Costa *et al.*, 2004) as suggested by the fact that sets of deep active dives are followed, for some individuals, by sets of drift dives. Therefore, the proportion of deep active dives in intensive and extensive foraging areas (ca. 45%) could be an average threshold of southern elephant seals' ability to dive deeply and actively without energetic pay-off (Davis *et al.*, 2001; Costa *et al.*, 2004).

Regarding the existence of two active dive classes, differences in their proportions were observed between day and night. But since deep and shallow active dives are both displayed during day and night time, a diel pattern cannot be the only explanation for their display. Besides diving physiology, a combination of biologic and oceanographic reasons can explain the existence of two distinct types of active dives. Previous studies have shown that female southern elephant seals feed on myctophids in the interfrontal zone (Ducatez *et al.*, 2008; Cherel *et al.*, 2008). Myctophids are bioluminescent cryptic fish and their habitat is highly dependent on light level (Widder, 2010). They adjust their habitat depth according to the light intensity and display not only nycthemeral migrations but also migrations in the water column depending on the local

light attenuation (e.g. depending on the particles concentration in the surface water layers, cloud cover, moonlight intensity etc.). Furthermore, the pelagic waters of the interfrontal zone include a variety of water masses (subtropical, subantarctic, polar water masses etc.) that host different prey species for southern elephant seals. The variety in prey, and their respective habitats, potentially drives different foraging behaviours. Interfrontal zones are major components in terms of biological production and are frequently populated with intense mesoscale eddies (Bakun, 2006). Vertical movement of water masses associated with cold-core eddies can induce isopycnal shoaling that is likely to influence prey behaviour, driving upward migrations to remain at preferred densities and temperatures (Wiebe, 1982). Cold water and high biomass in the surface layers may cause a decrease of luminosity contributing to the presence of the cryptic myctophids species at shallower depths (Flierl & McGillicuddy, 2002). Upward cold water masses, often from cyclonic eddies' cores and anticyclonic eddies' edges (Bakun, 2006), have been found to be preferential marine structures for foraging predators (Bost *et al.*, 2009; Bailleul *et al.*, 2010b; Dragon *et al.*, 2010). Female southern elephant seals were shown to clearly intensify their diving effort and decrease their diving depth in rich upwelling areas (Dragon *et al.*, 2010). Therefore, the existence of two active dive classes can be interpreted as a direct adaptation to the highly dynamic and heterogeneous pelagic waters where the seals forage. On the other hand, the increase of shallow active dives in areas of intensive foraging likely highlight the increased accessibility of prey in the water column as observed in previous studies (Dragon *et al.*, 2010). In cyclonic cores and anticyclonic edges where myctophids migrate to shallower depths, we can therefore expect the seals to display higher proportions of shallow active dives. Proportions of drift dives also varied accordingly: while intensively foraging, the seals displayed more drift dives. This could highlight their need, after displaying numerous active dives, either for resting or for food processing (Biuw *et al.*, 2003). In contrast, when the seals are extensively foraging and abundantly displaying exploratory dives, the diminution of drift dive proportions suggests either a low energy consumption prospective mode adopted

during the exploratory dives or, simply, less need for food processing. Either way, the ultimate proxy of the seals overall successful foraging, the mass gain, was significantly correlated with the percentage of intensive foraging mode and of active dives while in intensive foraging: the more numerous the active dives while intensive foraging, the more successful the foraging seals. Although we worked on a 1-year sample, similar results were found on numerous post-moulting and post-breeding tracks of northern elephant seals by Robinson *et al.* (2010). It should finally be noted that these significant correlations highlight the proxies' pertinence to predict, at the track scale, the foraging success of seals. Our sample of post-breeding females was selected to be homogeneous in mass and length so that the females could be supposed to have similar age and amount of experience. All went to forage in the interfrontal zone but displayed, in the end, a variety of mass gain, ranging from a loss of 60 kg to the gain of more than 100 kg in only 3 months. This high inter-individual variability in mass gain probably drives a fitness variability related to inter-individual variations in foraging behaviour and/or differences in prey selection (Field *et al.*, 2004, 2007). This confirms the importance of the individual foraging efficiency, and past experiences, in this dynamic and unpredictable oceanographic environment (Hindell *et al.*, 1999; Bradshaw *et al.*, 2004).

4.3 Methodological perspectives

Direct information on prey distribution remains very scarce in the Southern Ocean. Therefore, identifying periods of intensive foraging appears to be an efficient way to investigate the prey distribution of marine predators. Animal behaviour, in the horizontal and the vertical dimension, can be modeled as a dynamic variable changing in relation to the animal's internal state and/or its environment (Morales *et al.*, 2004; Jonsen *et al.*, 2007). Track-based analyses of the fine scale vertical behaviour could be an interesting next step to investigate relationships between seals behaviour and their environment. This could be used to systematically detect behavioural transitions along the dive profiles, associate them with the animal's direct

surroundings and infer information on prey distribution.

On the other hand, there are difficulties of interpretation of 2-dimensional data (time and depth) into a behaviour occurring in 4-dimensions (time-longitude-latitude-depth, Thums *et al.* (2008)). Brillinger & Stewart (1997) have shown that a time-depth curve can actually correspond to different possible 4D paths. We can therefore expect the same differences between the observed horizontal trajectory (longitude-latitude) and the actual path of a diving animal. Other studies have also questioned the validity of behavioural interpretations based on dataset with reduced dimensions (Harcourt *et al.*, 2000; Davis *et al.*, 2003). New technological devices, such as 3D-accelerometers and video cameras, are promising to solve those issues. In free-ranging Weddell seals (*Leptonychotes weddellii*) for instance, studies using video recordings have proved the encounter of prey within the foraging dives (Davis *et al.*, 2003). In Weddell seals and also in captive Steller sea lions (*Eumetopias jubatus*), accelerometers were able to precisely detect the mouth opening events linked with prey capture attempts (Naito *et al.*, 2010; Viviant *et al.*, 2010). Such *in situ* recording devices will indicate the real behavioural activity and also help to identify accurate 2-dimensional proxies of the foraging effort. Uses of such new devices could therefore validate our findings on active dives being the most successful foraging dives. It is our intention to examine this in future work.

5 Conclusion

Previous studies have shown that southern elephant seals display various behavioural modes detected from tracking data (Bailleul *et al.*, 2008) and various dive classes during their foraging trip (Hindell *et al.*, 1991; Thums *et al.*, 2008). Here we have shown that proportions of dive classes displayed by southern elephant seal females varied according to their horizontal behaviour. It is probable that by going to the polar frontal zone where resources are both spatially and temporally highly variable, female elephant seals can concentrate their foraging

474 searching activity in the most productive parts of the zone and maximise feeding success. They
475 repeatedly adapt their diving behaviour to prey accessibility in the water column and seem to
476 display a trade-off between diving depth and recovery time. Mass gain over the animals'
477 foraging trip was also highly correlated to the proportions of intensive foraging detected with
478 track-based analyses. Improved body condition of seals was finally associated with the
479 occurrence, within the vertical dimension, of sets of highly active dives. The classification of
480 diving behaviour is not an end in itself, but rather a tool that allowed us to conclude that
481 intensive foraging detected from surface tracking data is a good predictor of the diving activity
482 and foraging success occurring in the vertical dimension. However, in changing environments,
483 the addition of fine-scale monitoring of *in situ* oceanographic conditions to high resolution
484 behavioural datasets is an interesting further step in research on foraging behaviour in relation
485 to prey distribution.

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Variable	Abbreviation	Definition	Source
Bottom-Time (mn)	Bott.Time	descent end to ascent start	TDR
Bottom-Time Residuals (mn)	Res.Bott.Time	residuals of multiple regression	TDR
Maximum diving depth (m)	Max.Depth	-	TDR
Sinuosity	-	derived from Weimerskirch *et al.* (2007)	TDR
Ascending Speed (m/s)	Asc.Speed	-	TDR
Descending Speed (m/s)	Des.Speed	-	TDR
Horizontal Distance (km)	Horiz.Dist	distance travelled between 2 dives	GPS

Table 1: Behavioural variables: unit, abbreviation name, definition and source.

	Drift	Exploratory	Shallow Active	Deep Active
N =	2846	6221	12482	17656
Bott.Time (mn)	15.8 ± 6.0	11.3 ± 4.8	13.2 ± 3.3	10.1 ± 3.6
Res.Bott.Time (mn)	2.6 ± 5.9	-0.6 ± 4.7	0.7 ± 2.8	-1.2 ± 3.2
Max.Depth (m)	424 ± 118	348 ± 156	324 ± 127	698 ± 131
Sinuosity	0.29 ± 0.05	0.35 ± 0.08	0.41 ± 0.06	0.52 ± 0.04
Asc.Speed (m/s)	1.21 ± 0.22	1.31 ± 0.24	1.77 ± 0.19	1.56 ± 0.15
Des.Speed (m/s)	1.18 ± 0.37	1.22 ± 0.27	1.74 ± 0.26	1.76 ± 0.25
Horiz.Dist (km)	0.98 ± 0.74	1.57 ± 0.67	1.20 ± 0.32	0.97 ± 0.54

Table 2: Characteristics of dive classes for all individuals. All differences, between the dive classes, are statistically significant ($p < 0.001$). Bott.Time stands for bottom time and Res.Bott.Time for bottom time residuals (both in minutes). Max.Depth corresponds to the maximal depth of the dive. Asc.Speed and Des.Speed stand respectively for ascent and descent speeds. Finally Horiz.Dist corresponds to the horizontal distance travelled by the animal during its dive estimated from the tracking data.

ind	N	%Drift	%Exploratory	%Shallow Active	%Deep Active	% Active
09-78524	2605	14.8	9.6	2.5	73.1	75.6
09-78525	4169	9.4	12.2	28.8	49.6	78.4
09-86372	5778	5.3	15.5	41.4	37.8	79.2
09-86373	4325	9.2	12.2	47.3	31.3	78.6
ft03-Cy1-09	4219	4.6	24.6	34.2	36.6	70.8
ft03-Cy2-09	4843	5.9	6.7	41.5	45.9	87.4
ft03-Cy4-09	4889	5.9	12.5	42.9	38.7	81.6
ft03-Cy5-09	5450	5.6	31.3	32.9	30.2	63.1
ft03-Cy11038-09	4485	8.1	9.8	10.2	71.9	82.1
all ind	40763	7.7 ± 3.2	14.9 ± 7.9	31.3 ± 15.4	46.1 ± 16.1	77.4 ± 7.0

Table 3: Proportions of dive classes for all individuals (%) equipped in October 2009. Only dives located in the pelagic part of the tracks were classified. Overall, inter-individual variability can be noticed. But deep active dives tend to always be the most important dive class and active dives, combined deep and shallow classes, represent for each individual over two thirds of the whole dives. Drift dive class rarely reach 10% of the whole dives.

Dive Class (t)	Drift (t+1)	Exploratory (t+1)	Shallow Active (t+1)	Deep Active (t+1)
Drift	0.70	0.12	0.05	0.13
Exploratory	0.06	0.60	0.19	0.15
Shallow Active	0.01	0.09	0.76	0.14
Deep Active	0.02	0.05	0.11	0.82

Table 4: Observed probabilities of dive class changing from dive at time t to dive at time (t+1). High temporal persistence in the dive classes can be noticed and the second highest probabilities of dive class changing always correspond to the nearest dive class in terms of activity. Probabilities of changing reveal thus the hierarchy in the dive classes activity: an animal displaying a deep active dive is more likely to continue displaying this class of dive or to change for a shallow active dive and vice versa.

Model Formula	AICc
$MassGain \sim MassStart + DriftRateGain + FinalDriftRate + PropARS + PropActiveARS$	111.25
$MassGain \sim MassStart + DriftRateGain + PropARS + PropActiveARS$	87.27
$MassGain \sim MassStart + DriftRateGain + PropActiveARS$	75.61
$MassGain \sim DriftRateGain + PropActiveARS$	69.47
$MassGain \sim DriftRateGain$	65.99

Table 5: Model selection based on small sample sizes corrceted AIC. The model with the smallest AICc is considered the best. The variable to explain is the gain in mass over the animal's foraging trip and the tested variables are: the animal mass when equipped before the post-breeding foragfing trip (MassStart), the gain in drift rate over this trip (DriftRateGain), the final drift rate (FinalDriftRate), the percentage of intensive foraging mode in pelagic waters (PropARS) and the percentage of active dives displayed while the animal was in intensive foraging (PropActiveARS).

Figure 1: Physical oceanography in the Southern Indian Ocean and post-breeding foraging trips of 9 female southern elephant seals equipped in October 2009 (solid black lines). Light grey shading indicates depths less than 1,000 meters and depicts Kerguelen and Crozet plateaux. Îles Kerguelen and îles Crozet coastline's contour are also indicated in white over the plateaux. Dotted lines symbolized fronts (Orsi *et al.*, 1995), within the Southern Ocean: Southern SubTropical Front (SSTF), Sub-Antarctic Front (SAF), Polar Front (PF) and Southern Antarctic Circum-Polar Front (SACCF). In this study, we refer to the interfrontal zone as the area between the STF and the PF. Locations of intensive foraging behaviour displayed by the seals are indicated in dark grey dots over the tracks.

Figure 2: Characteristics of dive classes for all individuals: drift dives (dark green), exploratory dives (light green), shallow active dives (yellow) and deep active dives (orange). (a) Variations of bottom time residuals: drift dives are the longest dives while deep active present negative bottom time residuals. (b) Proportion of dive classes by day and night times: all classes occur by day and by night time. (c) Variations of maximum diving depth in function of bottom time: depending on maximum depth distribution, time spent at the bottom of the dives varies from one dive class to another. (d) Variations of sinuosity at the bottom of the dive in function of the ascending speed: the higher the sinuosity, the more important the ascending speed.(e) For each dive class, the density distribution of the descending speeds. The distribution similarity of descending speed for the two active dive classes can be noticed meanwhile exploratory and drift dives present low descending speeds. Finally, (f) distributions of the horizontal distance travelled during the dives: in exploratory dives, seals tend to swim more rapidly in the horizontal dimension than for the other dive classes. The dashed vertical lines indicate, for each dive class, the average horizontal distance.

Figure 3:

(a) Typical Depth-Time profiles of the four dive classes. (b) Locations of the dives along the seals' tracks. Orange dots correspond to deep active dives, yellow to shallow active, light green to exploratory dives and finally dark green to drift dives. All dive classes occurred all along the tracks, by day as well as by night.

Figure 4: (a) and (b) Proportions of dive classes in extensive parts (N = 15,081 dives) vs. intensive foraging parts of the tracks (N = 11,463 dives). Combination of deep and shallow active (hereafter referred as active classes) is more important in intensive foraging areas than in extensive ones.

Figure 5: For all individuals, mass gain presented with (a): overall drift rate, final drift rate and (b): percentage of time spent in intensive foraging and proportion of active dives realised in intensive foraging. Lines correspond to the significant linear regressions between variables.

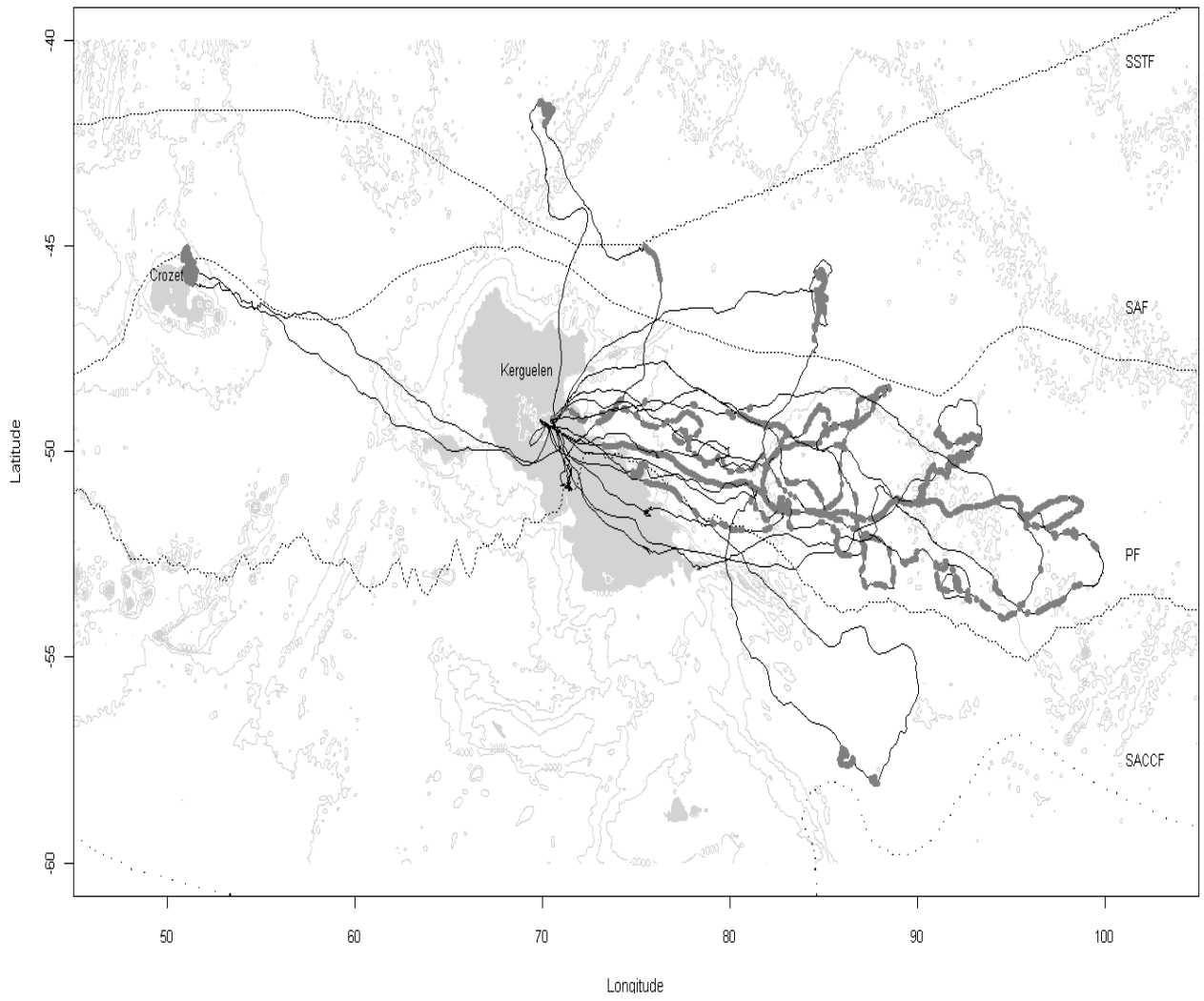
SSTF
SAF
PF
SACCF
Crozet
Kerguelen
Latitude
Longitude
-40
-45
-50
-55
-60
50
60
70
80
90
100

Figure 1:

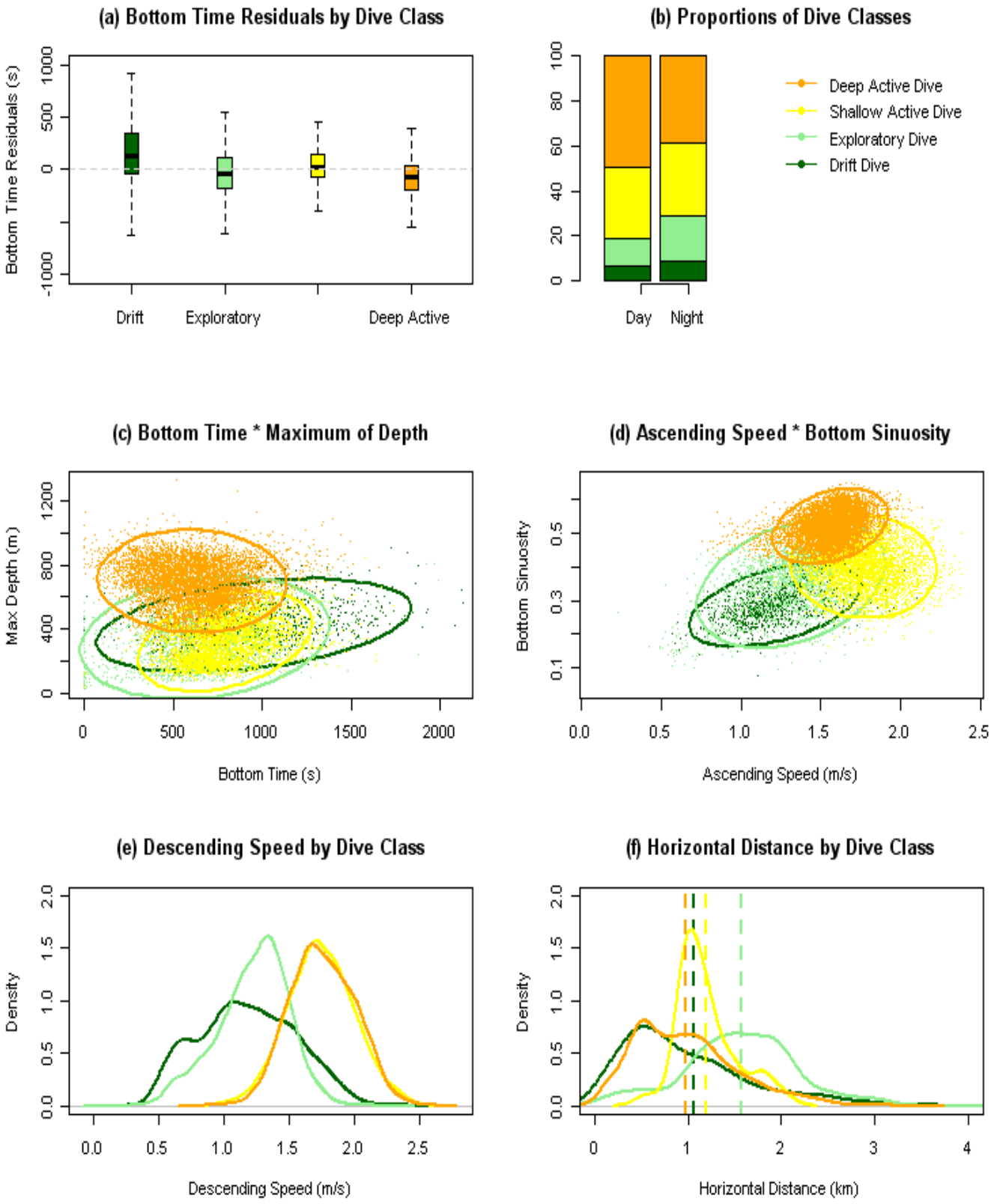
(a) Bottom Time Residuals by Dive Class
Bottom Time Residuals (s)
1000
500
0
-1000
Drift
Exploratory
Deep Active
(b) Proportions of Dive Classes
100
80
60
40
20
0
Day
Night
Deep Active Dive
Shallow Active Dive
Exploratory Dive
Drift Dive
(c) Bottom Time * Maximum of Depth
Max Depth (m)
1200
800
400
0
0
500
1000
1500
2000
Bottom Time (s)
(d) Ascending Speed * Bottom Sinuosity
Bottom Sinuosity
0.5
0.3
0.1
0.0
0.5
1.0
1.5
2.0
2.5
Ascending Speed (m/s)
(e) Descending Speed by Dive Class
Density
2.0
1.5
1.0
0.5
0.0
0.0
0.5
1.0
1.5
2.0
2.5
Descending Speed (m/s)
(f) Horizontal Distance by Dive Class
Density
2.0
1.5
1.0
0.5
0.0
0
1
2
3
4
Horizontal Distance (km)

Figure 2:

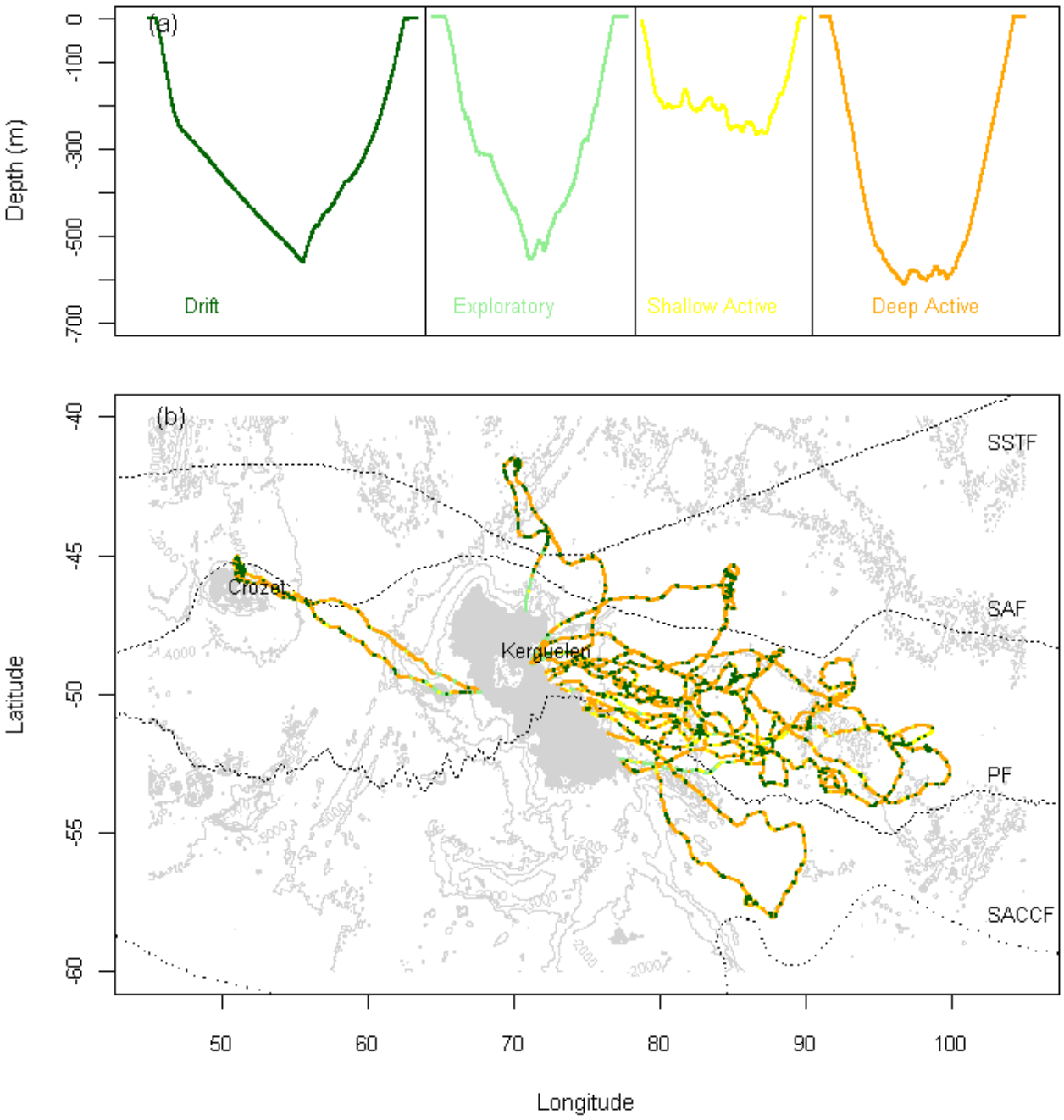
(a)
Depth (m)
0
-100
-300
-500
-700
Drift
Exploratory
Shallow Active
Deep Active
(b)
Latitude
-40
-45
-50
-55
-60
SSTF
SAF
PF
SACCF
Crozet
Kerguelen
4000
2000
50
60
70
80
90
100
Longitude

Figure 3:

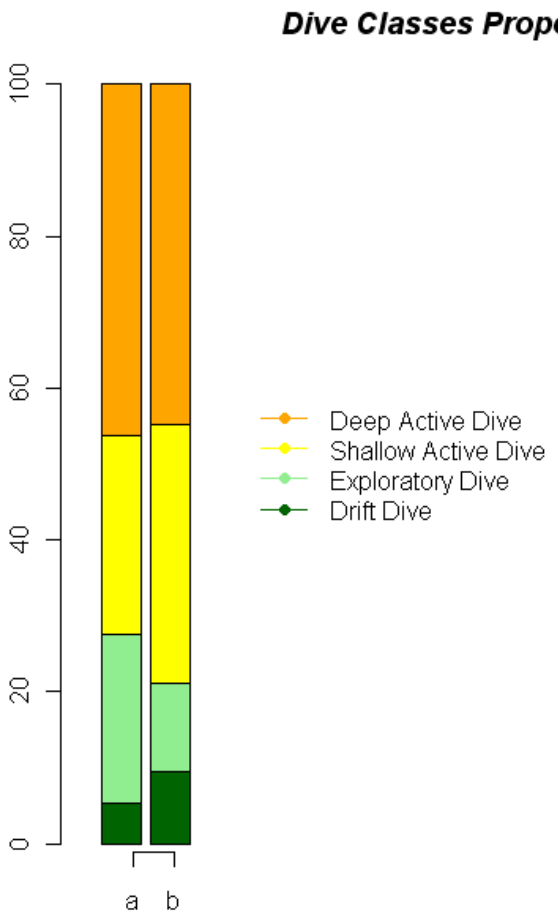
Dive Classes Proportions (%)
100
80
60
40
20
0
a
b
Deep Active Dive
Shallow Active Dive
Exploratory Dive
Drift Dive

Figure 4:

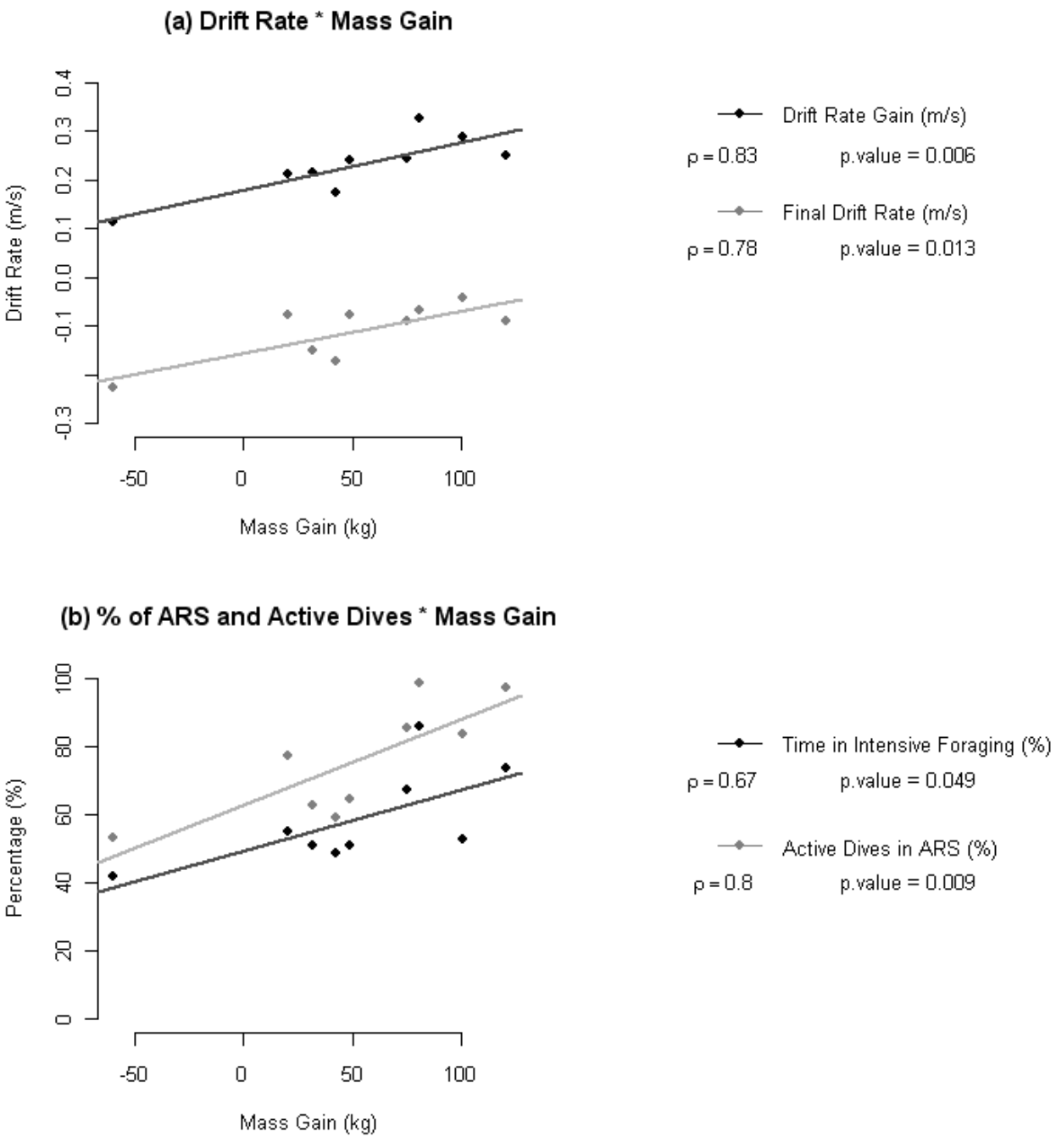
(a) Drift Rate * Mass Gain
Drift Rate (m/s)
-0.3
-0.1
0.0
0.1
0.2
0.3
0.4
-50
0
50
100
Mass Gain (kg)
Drift Rate Gain (m/s)
ρ = 0.83
p.value = 0.006
Final Drift Rate (m/s)
ρ = 0.78
p.value = 0.013
(b) % of ARS and Active Dives * Mass Gain
Percentage (%)
0
20
40
60
80
100
-50
0
50
100
Mass Gain (kg)
Time in Intensive Foraging (%)
ρ = 0.67
p.value = 0.049
Active Dives in ARS (%)
ρ = 0.8
p.value = 0.009

Figure 5: